



STUDIES ON THE PHYSIOLOGY OF CORALS

III. ASSIMILATION AND EXCRETION

BY

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WITH ONE TEXT-FIGURE AND ONE PLATE

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I. INTRODUCTION.

THE foregoing paper in this series confirmed and extended previous observations which showed that in the Madreporaria, as in other Coelenterata, a preliminary extracellular digestion of protein is followed by absorption of the fluid products of digestion, and by ingestion and intracellular digestion of small particles. Both of these processes are carried out in a definite "absorptive" zone in the mesenterial filaments. In this paper these processes and the subsequent process of excretion are followed histologically. The literature on the subject has been adequately reviewed in the previous paper. Acknowledgments are due to Mr. A. G. Nicholls for assisting in the collection of material used in this part of the research, and to Mrs. Yonge, who later assisted with the cutting of sections.

2. MATERIAL AND METHODS.

Feeding experiments to determine the site and course of absorption and intracellular digestion were carried out, using *Pocillopora bulbosa*, *Galaxea fascicularis*, *Psammocora gonagra* and *Symphyllia recta*. Subsequent sectioning revealed that *Pocillopora* was much the most suitable material, and this paper is largely concerned with the conditions observed in this coral. Small pieces of freshly collected, living coral were placed in large glass tanks containing sea-water, to which were added suspensions of blood from the small cat shark (*Chiloscyllium ocellatum*), common on the reef, and of finely chopped mollusc meat impregnated with colloidal "iron saccharate" (ferrum oxydatum saccharatum) or Indian ink. The corals were transferred to fresh sea-water at the end of four hours. Material was fixed at the end of the following periods after the suspensions had been added to the water: $\frac{1}{4}$, $\frac{1}{2}$, 1, 2, 3, 4, 6, 9 and 12 hours, and 1, 2, 3, 4 and 5 days. After feeding with blood-corpuses and meat impregnated with Indian ink, material was fixed with Bouin's fluid, and after iron saccharate with a mixture of equal parts of 90% alcohol containing 5% of ammonium sulphide and of Bouin's fluid. Material was also fixed in Carnoy's and Flemming's fluids for the detection respectively of glycogen and fat in the tissues.

Experiments on excretion involved the use of large, fleshy polyps. *Lobophyllia corymbosa* was accordingly used, suspensions of carmine in sea-water and of iron saccharate being injected into the thick edge-zone tissue by means of a hypodermic syringe. The polyps were then very rigorously washed in sea-water and transferred to jars containing clean water, being later examined and the tissues fixed after definite periods.

Sections were cut 6 and 8 μ thick, and were stained with Delafield's haematoxylin and erythrosin, or with iron-haematoxylin, mucicarmine and light green for the identification of mucus-glands, or with safranin and light green after fixation with Flemming. Mann's methyl blue and eosin were also used. For the demonstration of iron in the tissues, sections were treated with a 10% solution of potassium ferrocyanide and then with very dilute HCl, after which the tissues were stained with alum carmine.

3. STRUCTURE OF THE DIGESTIVE REGION.

The mesenterial filaments are the digestive organs of the Madreporaria. They contain the gland-cells which secrete the extracellular protease, while absorption and intracellular digestion take place exclusively within them. Figs. 1 to 4 show the structure of the mesenterial filaments of *Pocillopora* and *Lobophyllia* as seen in cross-section. The filaments consist of a glandular margin (figs. 1-4, *g.m.*), which is rounded in cross-section, and is usually sharply divided from the inner region (figs. 1-4, *i.m.*). Some authors have restricted the term mesenterial filament to the former region, but I here follow Boschma (1925) and many earlier workers, and use the word in its more general sense. The inner region of the filament is very thin except the part nearest to the glandular margin, where it swells out to about the same thickness as the margin. The thin innermost part of the mesenterial filaments is not shown in the figures. Within the whole of the inner region there runs a central strand of mesogloea (figs. 1-4, *m.*), which splits up within the glandular margin.

The glandular margin is composed of various types of cells. The bulk consists of a high columnar epithelium of supporting cells. These are ciliated, as observations on the

living tissues described in Paper I of this series have already demonstrated, but the cilia cannot be distinguished clearly in sections, and so are not shown in the figures. Amongst these cells are numerous gland-cells (figs. 1-3, *g.c.*), which contain rounded granules of secretion. There is every reason for assuming that these cells elaborate the extracellular protease, the properties of which were described in the foregoing paper. Mucus-glands (figs. 1-3, *m.g.*) are rather less numerous, and can easily be distinguished from the other gland-cells by their pink coloration after staining with mucicarmine, and by the reticular nature of the contained mucus. Finally there are nematocysts, either fully developed (fig. 1, *n.*) and situated in the outer layer of the epithelium, or in process of formation (fig. 3, *d.n.*) and deeper in the tissues.

The inner region of the mesenterial filaments is composed practically throughout of the same type of cell. These cells are larger than the supporting cells of the glandular margin, have very irregular free surfaces, and cell boundaries which cannot clearly be distinguished in sections; indeed Matthai (1923), who quotes earlier workers in support of this view, considers that the three layers of tissue or laminae in *Astraeid* corals are syncytial, and that there is "organic continuity between them." Runnström (1929), as a result of work on the histophysiology of the hydroid, *Clava squamata*, states that there the endoderm forms a syncytial plasma network which has important physiological functions both in connection with the absorption of food and also in its transport. Though observations on the living tissue show that cilia do occur in this region, they must be capable of retraction during the process of absorption. This phenomenon has been observed in *Hydra* by Greenwood (1888), and in a variety of *Lamellibranchia* by Potts (1923), and Yonge (1926*a*), in all cases in tissues which ingest and digest intracellularly. Mucus-glands rarely occur in this region in *Pocillopora*, but in *Galaxea* they are very abundant. In both genera, however, they are most numerous in regions more remote from the glandular margin, being very seldom found in the thickened region of the inner part of the filament. The "granular vacuoles" of Matthai occur occasionally in this region. Their function is unknown, but they may be akin to the wandering cells with granular contents described by Runnström in *Clava*. Zooxanthellae (fig. 2, *z.*) are present in this region, but their distribution will be described in detail in Paper IV in this series. They are never found in the glandular margin.

4. ABSORPTION.

Corals fed with meat and iron saccharate were sectioned to determine the site of absorption. Without exception absorption took place in the inner region of the mesenterial filaments, the so-called "absorptive" zone. It was never observed elsewhere. Much iron appeared in the coelenteron a quarter of an hour after the suspension was added to the water containing the corals, and a small amount of absorption was seen. The quantity of iron seen in the tissues rapidly increased, reaching a maximum at about the nine-hour stage, after which there was a small but distinct diminution. Absorption begins in the thickened distal portion of the inner region of the filaments. Later, as more material is absorbed, iron appears in the cells of the thinner, proximal part. This is shown in fig. 1, representing a mesenterial filament the glandular margin of which, owing to its frequent curves, has been cut through twice, and which was fixed 6 hours after being fed with iron. Great quantities of iron (*i.*) are seen in the tissues, especially in the

thickened part of the inner region next to the glandular margin. Absorption never takes place in the latter margin. Even in the earliest stages of absorption iron appears in the form of solid masses, as shown in fig. 1, and never as very fine particles or diffusely. This is the invariable manner in which this colloidal iron is taken into the tissues in animals which digest intracellularly, *e. g.* in Gastropoda as shown by Hirsch (1924) and in Lamellibranchia as shown by Yonge (1926*a*, 1926*b*, 1928), whereas in animals which exclusively digest extracellularly and where only the fluid products of this digestion can be absorbed by the cells, iron appears in the cells in a diffuse state, or as very fine granules, as observed by Steudel (1913) in Insecta, and by Yonge (1924) in Decapod Crustacea.

This localization of absorption within the inner or "absorptive" region of the mesenterial filaments in Madreporaria has already been experimentally demonstrated by Boschma (1925). Earlier workers, whom he quotes at length, had produced observational evidence pointing to this conclusion.

The mesenterial filaments remain heavily charged with iron for 2 or 3 days after feeding. There is then, as seen in sections, a very distinct diminution in the amount of iron in the tissues, and this is now, as shown in fig. 2 which represents a filament from a colony fixed 5 days after feeding, collected into large rounded masses (*i. e.*) in the region adjoining the glandular margin. Iron was also seen in process of being discharged into the lumen at this stage, and there is thus evidence, which will be extended later in this paper, to show that excretion as well as absorption takes place in this region. The secretion granules in the gland-cells (fig. 2, *g. c. i.*) are also coloured blue. This does not imply that excretion takes place by way of the gland-cells, but only that substances in solution in the body-fluids are taken out by the gland-cells together with material needed for the elaboration of the enzymes. This fact was originally established by Jordan (1904), working on *Astacus*, but similar conditions have been observed in a number of invertebrates, of which I have given details and references elsewhere (1926*a*). Boschma (1925) found that in *Astrangia* Indian ink absorbed along with food began to disappear from the tissues 5 days after feeding, and had completely vanished after 7 days.

5. INTRACELLULAR DIGESTION.

The occurrence of intracellular digestion in the mesenterial filaments, already indicated by the manner in which iron saccharate is taken in, was demonstrated conclusively by feeding corals with blood-corpuscles from elasmobranchs and with meat impregnated with Indian ink. The latter method was employed with success by Boschma, but only poor results were obtained with *Pocillopora*. Indian ink appeared in the tissues of the inner part of the mesenterial filaments, but only in very small amounts.

The experiments using blood-corpuscles gave more interesting results. Owing to the speed of digestion, already emphasized in the preceding paper, observations had to be made on tissues fixed very soon after feeding. Thus in *Galaxea*, though intact blood-corpuscles were seen on the disc, in no case could they be recognized in the coelenteron. More success was attained with *Pocillopora*, as shown in fig. 3, which represents the appearance of a mesenterial filament half-an-hour after it had been fed with a suspension of blood. One corpuscle (*b. c.*) in process of digestion is secured by mucus (*m. e.*) to the surface of the glandular margin and directly over two gland-cells. A gland-cell near is

discharging its secretion (*g.c.d.*). Digestion has only just begun, for the corpuscle is still intact, although the very faint staining of the cytoplasm with erythrosin indicates that it is being broken down by the extracellular protease secreted by the gland-cells. It is noteworthy that the corpuscles, which can be partially broken down by this initial extracellular digestion, are carried to this region of the mesenterial filaments, and that they are not necessarily presented to the cells of the inner region for direct ingestion.

After the digestion of the greater part of the cytoplasm the condensed nucleus of the corpuscles and the remaining cytoplasm are apparently carried round to the inner region of the filament, where they are ingested. This is indicated by the presence of condensed darkly staining masses (*i.b.c.*) lying inside vacuoles (*v.*) within the tissues in this region. Observations on *Psammocora* showed, however, that ingestion may be direct, for easily recognizable blood-corpuscles were identified within the "absorptive" zone twelve hours after the commencement of feeding. An attempt to follow the course of this intracellular digestion further by means of material fixed with Flemming's fluid proved unsuccessful owing to the presence normally in the tissues of numerous fat-globules, from which the fat in the half-digested corpuscles could not be distinguished.

Nevertheless, the results outlined above, together with the results of the experiments on the speed of digestion summarized in Table XVIII of the preceding paper, show clearly that intracellular digestion takes place in the inner part, or "absorptive" zone, of the mesenterial filaments and, like absorption, exclusively there.

6. RESERVE FOOD MATERIAL.

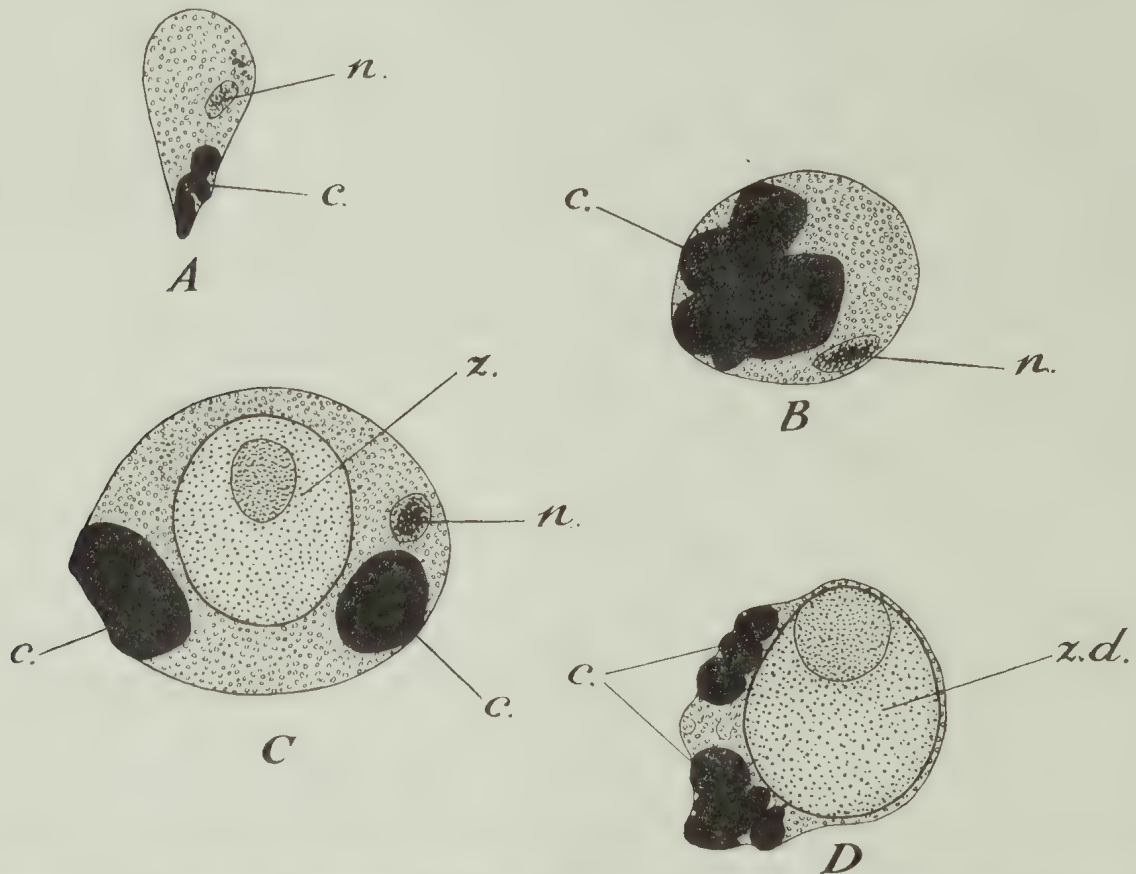
Although nuclei can occasionally be seen in the mesogloea, no evidence of the transportation of ingested food through it by wandering cells, such as Pratt (1906) found in fresh material of *Alcyonium*, was obtained by examination of sections. There is some reason for supposing that this takes place very largely either by direct passage from cell to cell or through a syncytium. There was no indication of the presence of glycogen in the tissues of *Pocillopora*, *Galaxea* or *Symphyllia*, after material fixed in Carnoy had been treated with iodine. Fat, on the contrary, is abundant in the tissues. Polyps of *Pocillopora* fixed in Flemming and sectioned were seen to contain numerous fat-globules in all endodermal tissues. They were most abundant in the mesenteries (except the glandular margin of the filaments), and somewhat less so in the endoderm within the tentacles. In all cases fat and zooxanthellae are found side by side, and in view of the possibility that fat may come from the zooxanthellae, wholly or in part, the detailed study of these regions is left to Papers IV and V of this series. There is practically no fat in the free ectoderm, but the epithelium lying against the skeleton and which secretes it contains immense numbers of large fat-globules.

7. EXCRETION.

No previous work has been done on excretion in Madreporaria, nor, apparently, in any Anthozoa other than *Alcyonium digitatum*. Pratt (1906), working on that species, found that carmine was excreted by the "amoeboid endoderm" cells of the mesenterial filaments. She also found carmine in the amoeboid cells of the mesogloea after animals had been kept for 3 days in water containing suspended carmine, and, as a result,

came to the conclusion that these cells "may also convey waste products to the coelentera or lumen of the canals."

The first experiment on *Lobophyllia corymbosa* consisted of injecting a suspension of carmine in sea-water into the edge-zone tissue and, after taking great care that no carmine entered the coelenteron, transferring the specimen to a jar of clean sea-water. After 24 hours the polyp was examined. Carmine was found in process of extrusion from the mouth in mucus-laden strings that contained dead zooxanthellae and other



TEXT-FIG. 1. *Lobophyllia corymbosa*, cells from "absorptive" zone of mesenterial filament from polyp injected $1\frac{1}{2}$ hours previously with a suspension of carmine in the edge-zone; tissue macerated by Hertwig's method. $\times 3000$. A and B, cells containing carmine prior to its excretion; C and D, cells with contained zooxanthella as well as carmine. c., carmine; n., nucleus of cell; z., zooxanthella; z.d., zooxanthellae in first stage of degeneration.

waste material. The mesenteric filaments were removed and examined, but no evidence of carmine was found in them or elsewhere in the endoderm.

Since excretion was apparently completed within 24 hours, a second experiment was carried out in which the tissues were examined at frequent intervals after the injections had been made. The same process was adopted, a number of polyps, all with a number of mouths, being injected. Samples were examined after $1\frac{1}{2}$, 3, 5 and 6 hours, both fresh and, where necessary, after maceration with Hertwig's method, using a mixture of 0.04% osmic acid and 0.2% acetic acid in sea-water and washing repeatedly in 0.2% acetic in sea-water. The results obtained are given below:

After $1\frac{1}{2}$ hours: One polyp was opened and examined. Some carmine was found in

the coelenteron mixed with mucus, etc. The mesenterial filaments were heavily laden with carmine, especially in the "absorptive" zone, where it was present in masses, together with some zooxanthellae. Carmine was also seen in the inner, thinner region of the mesenterial filaments, but never to the same extent. None was ever seen in the glandular margin, although excreted material was passed over it. Macerated material confirmed these findings, drawings of four cells from the "absorptive" zone being shown in Text-fig. 1. In two of these, A and B, the cells contain masses of carmine (c.) alone, but the other two, C and D, each contain a zooxanthella (z.), that in D showing clear signs of degeneration. Unlike Matthai, who, however, macerated only previously fixed material, invariably obtained well-defined cells after maceration. Further evidence and figures will be given in Paper IV.

After 3 hours: A little carmine could still be seen in fresh material within the cells of the "absorptive" region of the mesenterial filaments, but much less than after $1\frac{1}{2}$ hours, when the tissues were frequently stained bright red with it and when it was visible to the naked eye without the aid of the microscope. No carmine was seen in the other parts of the mesenterial filaments or in any other region, but it was very abundant in the coelenteron. The other pieces, awaiting later examination, were observed to be discharging carmine in masses mixed with mucus through the mouth.

After 5 hours: A polyp was examined which shortly before had been observed discharging a large mass of carmine through the mouth. Only a very little carmine was found within the coelenteron, and careful examination under the microscope failed to show the presence of carmine in a number of mesenterial filaments examined, except in one very small region where some traces remained.

After 6 hours: A few traces of carmine were found in the coelenteron, but the most careful search failed to reveal the presence of any in the mesenterial filaments.

Later a further experiment was carried out, polyps being fixed in Bouin's fluid $\frac{1}{4}$, $\frac{1}{2}$, $\frac{3}{4}$, 1, $1\frac{1}{2}$ and 2 hours after injection. This material was later sectioned. Carmine was found in the deeper tissues $\frac{1}{2}$ hour after injection, but owing to the difficulty of determining cell outlines in Madreporarian tissues after fixation, it was never possible definitely to prove that it was being carried by wandering cells, as Pratt found in *Alcyonium*. There appears to be every reason for thinking that such is the case, however, for the carmine appeared in the region of the mesogloea while, after $1\frac{1}{2}$ hours, it appeared exclusively in the cells of the mesenterial filaments.

The appearance of a mesenterial filament at this stage is shown in fig. 4. The site of carmine excretion is clearly shown. There is no trace of any in the glandular margin or in the mesogloea, but the cells of the inner part of the filament are loaded with it (c.e.), especially near their free margins, where it can be seen in process of excretion into the coelenteron and also free after excretion (c). The site of excretion in the distal or "absorptive" zone of the inner part of the mesenterial filaments, and its histological appearance, are identical with those of absorption.

Polyps were also injected in the same way with a suspension of iron saccharate in seawater and fixed in the usual manner. Iron was excreted in the same manner and in the same region as carmine, but it proved possible in this case to demonstrate its presence in wandering cells in the mesogloea while being transported from the edge-zone to the mesenterial filaments. Such a cell, from a polyp fixed $\frac{1}{2}$ hour after injection, is shown in fig. 5. This wandering cell was in the mesogloea within a mesenterial filament, and the

contained iron, which was apparently within small rounded vacuoles, is represented by the black dots.

8. DISCUSSION.

The mesenterial filaments are responsible for digestion, absorption and excretion in the Madreporaria. The glandular margin secretes the enzyme (protease), the properties of which were described in Paper II of this series, and which acts extracellularly in the coelenteron. It also possesses nematocysts and mucus-glands which aid respectively in the final destruction of the prey and in its transport by the cilia. The inner part of the filaments is concerned with absorption and intracellular digestion, which takes place particularly in the thickened region adjacent to the glandular margin, which has been known as the "absorptive" zone. The intracellular enzymes (protease, lipase and glycogenase) from this region were also studied in the preceding paper, where the presence of absorption in this region was first demonstrated. The great speed with which the digestion of protein takes place is further emphasized by the partial digestion of blood-corpuscles by *Pocillopora* within half an hour after they have been added to the water.

The name given to this zone is misleading, because excretion, as well as absorption, takes place exclusively here, as experiments described in this paper demonstrate conclusively. This region of the mesenterial filaments is thus apparently the only region in the body of a coral where interchange between the interior of the tissues and the exterior can take place. This fact will be found to be of great importance when the possible significance of the zooxanthellae in the life of the corals comes to be discussed.

Madreporaria do not apparently store glycogen in any discernible amount, but there are large reserves of fat. The transport of food material from the site of its absorption to the other tissues may sometimes be by way of wandering cells in the mesogloea and elsewhere, but this was not definitely proved, although it was found that material may be carried from the edge-zone to the mesenterial filaments for excretion by this agency. In the endoderm particularly, although the presence of definite cells was proved by maceration, in life material may be passed from cell to cell, or cell-walls may temporarily break down—as they certainly do on fixation—and syncytia be formed. Further research is needed before definite conclusions can be arrived at.

9. SUMMARY.

1. The mesenterial filaments constitute the digestive organs of the Madreporaria. They consist of a glandular margin which possesses gland-cells, which secrete the extracellular protease, and also possesses nematocysts and mucus-glands, and an inner region, which is concerned exclusively with absorption, intracellular digestion and excretion.

2. Experiments on absorption and intracellular digestion were carried out with *Pocillopora bulbosa* and *Psammocora gonagra*, and on excretion with *Lobophyllia corymbosa*.

3. Absorption takes place exclusively within the cells of the inner part of the mesenterial filaments, especially in the so-called "absorptive" zone, which is the thickened distal region adjacent to the glandular margin.

4. The fact that colloidal "iron saccharate" is absorbed in the form of large masses, and not diffusely, and that semi-digested red blood-corpuscles of elasmobranchs are

ingested, both in the cells of the "absorptive" zone, shows that intracellular digestion as well as absorption takes place here.

5. No glycogen was found in the tissues of any coral examined, but there are abundant reserves of fat both in the endoderm and especially in the ectoderm which secretes the skeleton.

6. Excretion of carmine and iron saccharate injected into the edge-zone tissue takes place exclusively by way of the cells of the "absorptive" zone, material being transported thence, at any rate partially, by wandering cells in the mesogloea. In other cases material may be passed from cell to cell or syncytia may be formed which permit its free passage.

7. The so-called "absorptive" zone of the mesenterial filaments is thus the only region of the coral where interchange between the interior of the tissues and the exterior takes place.

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DESCRIPTION OF PLATE I.

Lettering employed: *b.c.* Fed blood-corpuscle lying on surface of glandular margin of mesenterial filament. *c.* Carmine excreted into coelenteron. *c.e.* Carmine in process of being excreted from cells of inner region of mesenterial filament. *d.n.* Developing nematocyst. *g.c.* Gland-cell. *g.c.d.* Gland-cell discharging secretion. *g.c.i.* Gland-cell with secretion containing iron. *g.m.* Glandular margin of mesenterial filament (cilia not shown). *i.* Ingested iron. *i.b.c.* Ingested blood-corpuscle. *i.e.* Iron accumulated ready for excretion. *i.m.* Inner region of mesenterial filament. *m.* Mesogloea. *m.e.* Mucus on surface of glandular margin. *m.g.* Mucus-gland. *n.* Nematocyst. *n.b.c.* Nucleus of fed blood-corpuscle. *v.* Digestive vacuole. *z.* Zooxanthella.

FIG. 1. — *Pocillopora bulbosa*. Transverse section through convoluted region of mesenterial filament; glandular margin cut through twice. Fixed 6 hours after "iron saccharate" added to water. $\times 600$.

FIG. 2. — *Pocillopora bulbosa*. Transverse section through end of mesenterial filament 5 days after feeding with "iron saccharate." $\times 600$.

FIG. 3. — *Pocillopora bulbosa*. Transverse section through end of mesenterial filament $\frac{1}{2}$ hour after feeding with blood-corpuscles from cat shark, fixed Bouin's fluid stained Delafield's haematoxylin and erythrosin. $\times 600$.

FIG. 4. — *Lobophyllia corymbosa*. Transverse section through end of mesenterial filament $1\frac{1}{2}$ hours after polyp injected with a suspension of carmine into the edge-zone. Fixed Bouin's fluid, stained Delafield's haematoxylin. $\times 270$.

FIG. 5. — *Lobophyllia corymbosa*. Cell from mesogloea within mesentery containing fine, rounded masses of "iron saccharate" $\frac{1}{2}$ hour after this was injected into the edge-zone of the polyp. $\times 1200$.

GREAT BARRIER REEF EXPEDITION 1928-29.

Brit. Mus. (Nat. Hist.).

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PLATE I.

